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This volume is dedicated to Dr. Rainer Zangerl

Megapleuron zangerli
A New Dipnoan from the Pennsylvanian, Illinois

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ABSTRACT

Megapleuron rochei Gaudry 1881 from the lower Permian of France is redescribed. Small juvenile specimens from the Middle Pennsylvanian of Illinois are placed in the same genus as the new species *M. zangerli*. The genus differs from all other contemporaneous dipnoans in the arrangement of the bones in the skull roof.

INTRODUCTION

Denison (1969, pp. 208-209) described but did not name two juvenile dipnoans with the tooth-plates in an early stage of development. A few additional specimens of the species have since been collected. The best preserved specimen, chosen as the type of a new species, was given first to Dr. D. Baird, Princeton, who offered it to me for description during my stay at Field Museum, Chicago. After realizing that the pattern of the bones of the skull roof differs from that in *Sagenodus*, I found an identical pattern in the poorly preserved type and only specimen of *Megapleuron rochei* Gaudry 1881. The type specimen of *M. rochei* will be described first for proper comparison with the specimens from the Middle Pennsylvanian of Illinois.

During my stay at Field Museum, I prepared polysulfide rubber casts of all specimens. These casts and the specimens have been investigated in Field Museum and in the Geol.-Paläont. Institut of the University of Göttingen. I am much indebted to Dr. R. Zangerl for providing facilities for study in Field Museum. I wish to thank

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Dr. E. S. Richardson, Jr., Chicago; Dr. R. H. Denison, Lincoln, Mass.; and many private collectors in the Chicago area for their help and interest in my studies. In addition to the type specimen of *M. zangerli*, Dr. D. Baird, Princeton, was kind enough to offer me the specimen of *Ctenodus cristatus* described below. I thank Dr. D. Heyler, Paris, for sending a cast of the type specimen of *M. rochei* and for discussing the interpretation of the specimen. The technical assistance of Mrs. Badura, Miss L. Beyer, Mr. W. Kleinitzke, Mr. M. Sosnitza, Mrs. A.-L. Aubatzus, and Miss Wilgeroth is gratefully acknowledged. My thanks are also due to Dr. W. Riegel, Göttingen, and Dr. E. S. Richardson, Jr., Chicago, for improving the English of the paper.

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Abbreviations:

AMNH	American Museum of Natural History, New York
MHNP	Muséum National d'Histoire Naturelle, Paris
PU	Princeton University, Princeton, N.J.
PF	Field Museum of Natural History, Chicago, Fossil Fish collection

Private collections:

Dab	Mr. W. Dabasinskas, Monticello, Wisconsin
HTP	Mr. and Mrs. T. Piecko, Chicago, Illinois
R	Mrs. L. Rockwell, Chicago, Illinois
W	Mr. and Mrs. Francis A. Wolff, Port Charlotte, Florida. Much of the Wolff collection has been deposited in Field Museum.

The important collection of the late Mr. J. Herdina is now in Field Museum; it includes specimens PF 3200, PF 8369, and PF 8370.

SYSTEMATIC DESCRIPTION

Genus **Megapleuron** Gaudry 1881

Type species.—*Megapleuron rochei* Gaudry 1881

Diagnosis.—Dipnoan genus with unconstricted notochord; neural spines and (around 30) ribs are developed. The continuous dorsal fin extends far rostrad. Thin round scales. Skull-roof: an unpaired E-bone in front of the pair of C-bones; B-bone large compared with the lateral bones I, J, Z, and Y; the supraoccipital cross-commissure passes near the posterior border through B. Toothplates similar to *Sagenodus*.

Age.—Upper Carboniferous (Middle Pennsylvanian)—Lower Permian (Lower Autunien).

Comparison.—Gaudry (1881a), describing the first and only specimen of the type species, founded the new genus *Megapleuron* on the supposed main feature, "rhombic scales," in which the specimen differed from all other post-Devonian dipnoans. After Fritsch (1888) suggested that these scales belonged to a palaeoniscoid fish, Sauvage (1893) described round scales, but he confirmed the view point of Gaudry (1881a) that *Megapleuron* is related to *Neoceratodus* because of the shape of the scales and the tooth plates. Fritsch (1888) considered *Megapleuron* to be a synonym of *Ctenodus* because of the size and shape of the ribs. Nevertheless, the opinion of Woodward (1891) in synonymizing *Megapleuron* with *Sagenodus* has since been accepted.

Postcranial features are not distinctive enough in post-Devonian lungfishes to be useful in separating genera. Useful features are the pattern of the bones in the skull roof and the tooth plates. The bone pattern in the skull roof of post-Devonian dipnoans is very constant in comparison with Devonian forms (Westoll, 1949, p. 153). The figure of *Megapleuron* given by Gaudry (1883) already shows a skull roof with a pair of bones (C) in front of a large occipital bone (B), a feature separating *Megapleuron* from *Sagenodus*. *Sagenodus* is characterized by an unpaired B- and an unpaired C-bone (Watson and Gill, 1923, fig. 1). In contrast to *Ctenodus*, which has a pair of C- and of E-bones, *Megapleuron* has a round, large, unpaired E-bone rostrad to the pair of C-bones. Thus, *Megapleuron* is clearly distinct from both *Sagenodus* and *Ctenodus* in the bone pattern of the skull roof. The large B-bone in combination with small J and I is typical for only *Megapleuron* among post-Devonian dipnoans, but comparison is possible with some specimens of the Devonian *Phaneropleuron* (Westoll, 1949, fig. 7A) which also have unpaired E-bones. The relation between J, KX, L, M, and C is comparable also with the pattern in *Phaneropleuron* and *Scaumenacia*. Gaudry (1881a, p. 753) compared *Megapleuron* with *Phaneropleuron* because of the ribs, an insignificant feature.

The tooth plates of *Megapleuron* seem to be close to tooth plates of the *Sagenodus* type (*Sagenodus*, *Tranodis*) with the difference that a gap is developed between the first and second tooth ridges in the lower tooth plates. Great differences exist between *Megapleuron* (fig. 5) and *Sagenodus* in the shape of the parasphenoid, the entopterygoids, and the relation between them. The rostral part of the

FIG. 1. *Megapleuron rochei* Gaudry, rubber cast from the head of the type specimen MHNP -; Lower Permian/Igornay, France. × 0.6.

parasphenoid is larger in *Megapleuron* and extends farther rostrad between the entopterygoids than in *Sagenodus*. The entopterygoids do not surround the lateral edges of the parasphenoid, and the parasphenoid possesses a shorter posterior process than that in *Sagenodus* (Watson and Gill, 1923, fig. 10). These features also distinguish it from *Ctenodus* (Watson and Gill, 1923, fig. 26).

Megapleuron rochei Gaudry 1881. Figures 1, 2.

Megapleuron Rochei. Gaudry, A., 1881a, C. R. Acad. Sci. Paris, 92, pp. 752-754; 1881b, Bull Soc. géol. France (3), 9, p. 299; 1883, Les Enchainements du Monde animal dans les Temps géologiques: Fossiles Primaires, pp. 238-239, fig. 246; 1888, Mém. Soc. Nat. Autun (1888), pp. 3-7, 1 fig.; Fritsch, A., 1888, Fauna der Gaskohle und der Kalksteine der Permformation Böhmens, 2, Heft 3, p. 65, fig. 143; Sauvage, H.-E., 1890, Etudes des Gîtes Minéraux de la France; Bassin houiller et permien d'Autun et d'Epinac, fasc. III, pp. 27-28, pl. V, fig. 1; 1893, Etudes des Gîtes minéraux de la France: Bassin houiller et permien d'Autun et d'Epinac, fasc. V, pp. 28-29; 1894, Bull. Soc. Hist. Nat. Autun, pp. 59-62; Wood-

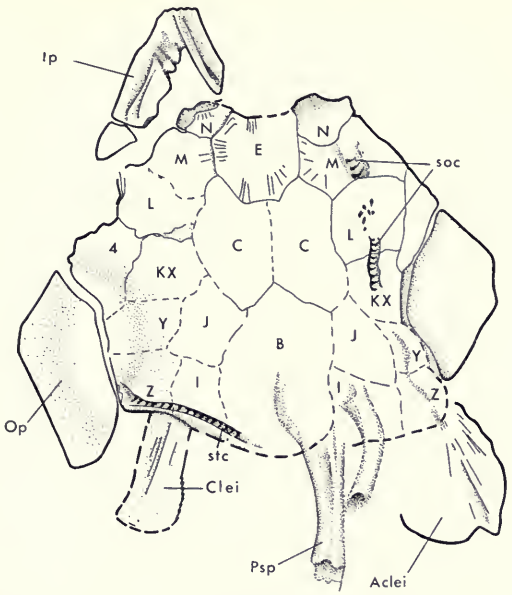


FIG. 2. *Megapleuron rochei* Gaudry, skull roof of the type specimen MHNP-, dorsal view; lower Permian/Igornay, France. ×½. B, C, E, I, J, KX, L, M, N, Y, Z, bones of the skull roof; *4*, bone of the cheek region; *Aclei*, anocleithrum; *Clei*, cleithrum; *Op*, opercular; *Psp*, parasphenoid; *soc*, supraorbital canal; *stc*, supraoccipital commissure; *tp*, tooth plate presumably of the lower jaw.

ward, A. S., 1891, Catalogue of the fossil fishes in the British Museum, Part II, p. 262.

Sagenodus rochei. Heyler, D., 1969, Cah. paléontol. (1969), p. 245 (footnote).

Type.—One unnumbered specimen in the Muséum national d'Histoire naturelle, Paris (figs. 1, 2; Gaudry 1883, fig. 246; Fritsch 1888, fig. 239, Sauvage 1890, pl. V, fig. 1).

Horizon.—Beds of Igornay, Lower Autunien, Lower Permian.

Locality.—Igornay, Dépt. Saône-et-Loire, France.

Diagnosis.—E-bone small compared with C and B; rostral-abrostral length of E to the length of B nearly 1:2, rostral-abrostral length of C to the length of B 4:5.

Comparison.—See *M. zangerli.*

Description.—The type specimen shows the trunk very well, but the head is poorly preserved (fig. 1). The specimen is flattened dorso-ventrally, with the dorsal side exposed. The trunk of the spec-

FIG. 3. *Megapleuron zangerli* n. sp., type specimen R 5323 in ventral view; Middle Pennsylvanian/Pit 11, Will and Kankakee Counties, Illinois. × 4.

imen was figured by Gaudry (1883, fig. 246) and described by him (1881a, p. 753) sufficiently well so that only an interpretation of the skull roof will be given here.

The bone best recognizable on the skull roof (fig. 2) is E with sutures to C, M, and N, and with lines directed toward the radiation-center. The sutures of C, N, M, L, and KX can be restored with reasonable accuracy but all sutures behind C and KX are a matter of interpretation; they are restored by comparison with the small specimens from Illinois. The rostral suture of B against the pair of C-bones could be restored, and because B has to extend far abrostrad to include the supraoccipital commissure (*stc*), B is consequently a very long bone on the skull roof. The sensory line system is very poorly preserved, and only parts of the supraorbital canal (*soc*) and the supraoccipital commissure could be found. J and KX border the C-bones on the posterior-lateral side; L and M lie lateral and rostrolateral to E. In front of the skull roof the impression of a tooth plate (*tp*), possibly the tooth plate of the lower jaw, can be seen in lateral view.

A blade-like bone (*Aclei*) is partly shown on the right side behind the skull roof. This anocleithrum has a form comparable to the equivalent bone in *Sagenodus* (Watson and Gill, 1923, fig. 17 A, B: "post-temporal"). The left cleithrum (*Clei*) is the only other bone of the shoulder girdle which is partly preserved. Behind the cleithrum, (?) two cranial ribs articulate to the occipital region of the endocranium below the parasphenoid (*Psp*).

Megapleuron zangerli n. sp. Figures 3-9.

1969 undetermined dipnoan—Denison, New Pennsylvanian lungfishes from Illinois, pp. 208-209, fig. 110.

Type.—R 5323, a small, nearly complete fish preserved in counterpart (figs. 3, 4).

Referred specimens.—PF 5707 (Denison, 1969, fig. 110), the smallest specimen; all following specimens preserved in part and counterpart: PF 8329, PF 3200, the largest specimen (figs. 7, 8); PF 8370; PF 8369 (fig. 9 A); W 118 (fig. 9B); Dab without number (fig. 5); HTP 5701.

Horizon.—Francis Creek Shale, Carbondale Formation, Middle Pennsylvanian.

Locality. — Pit 11 of the Peabody Coal Company, Will and Kankakee Counties, Illinois, USA (see: Richardson and Johnson, 1971).

Diagnosis. — Large E- and B-bone, C-bones smaller. Rostral-abrostral length of E to the length of B between 4:5 and 3:4, rostral-abrostral length of C to the length of B 2:3.

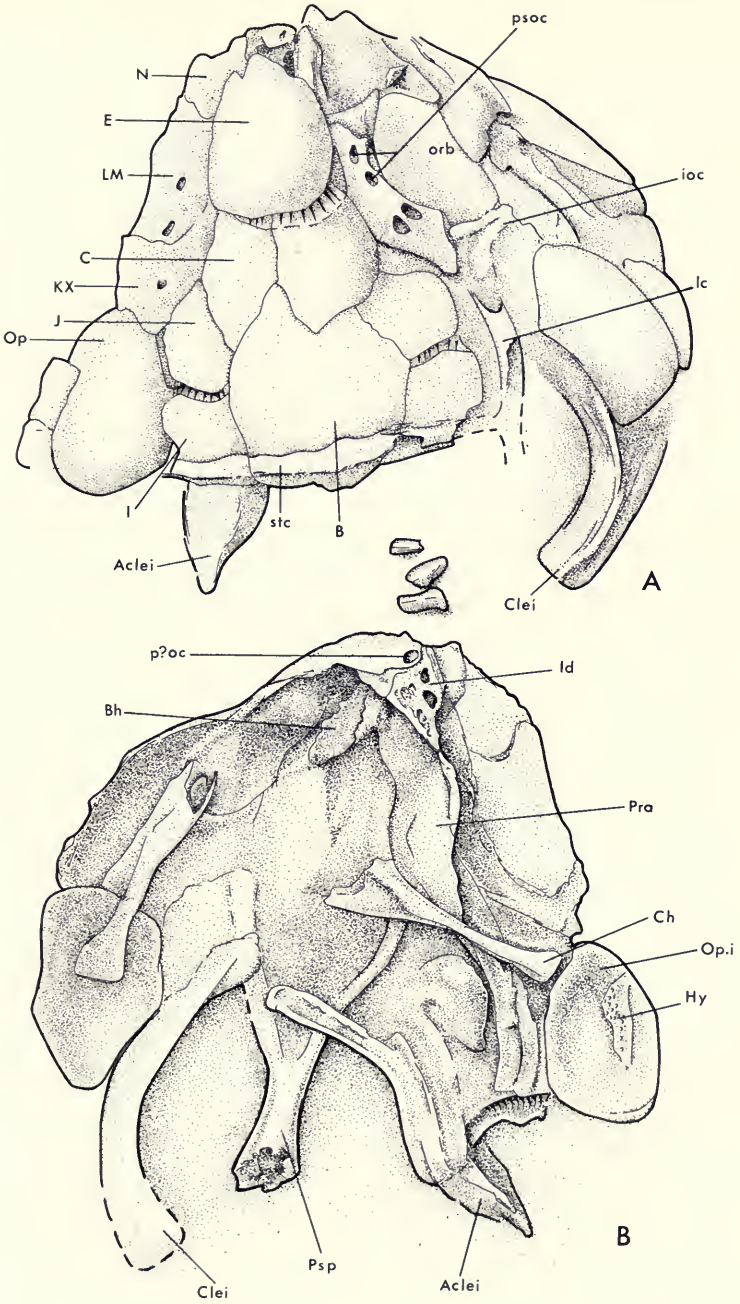
Comparison. — A comparison between the large specimen of *M. rochei* and the juvenile specimens of *M. zangerli* is difficult. The main difference lies in the size of E in comparison to other bones in the skull roof. E is smaller in *M. rochei*, a difference which should be valid between *M. rochei* and adult specimens of *M. zangerli* even taking in consideration that the length ratio between E and B varies from 4:5 in the type specimen of *M. zangerli* to 3:4 in the larger specimen PF 3200. This shows that the posterior portion of the skull roof displays a positive allometry with respect to the rostral portion. If B is restored correctly in *M. rochei* and *M. zangerli*, B is much broader in *M. zangerli.*

TABLE 1

Specimen	Total length (mm)	Length of head (mm)	Remarks
PF 5707	>16	5	smallest specimen
W 118	21	6	
HTP 5701	>32	8	
PF 8369	37	8	
R 5323	>46	9	type specimen
PF 8370	>>35	10	
PF 8329	65	10	
Dab -	>>40	12	
PF 3200	>>43	15	largest specimen

Description. — All known specimens are juvenile, and rarely is a whole specimen preserved in the nodule (table 1). The ratio of length of the head to total length varies from 1:3 to 1:5, demonstrating the normal positive allometric growth between body and head from young to adult specimens. The positive allometric growth ratio be-

FIG. 4. *Megapleuron zangerli* n. sp., type specimen R 5323 Middle Pennsylvanian/ Pit 11, Will or Kankakee County, Illinois. × 8. A, skull roof in dorsal view (drawn from rubber cast). B, head in ventral view (drawn from rubber cast). B, C, E, I, J, KX, LM, N, bones of the skull roof; *Aclei*, anocleithrum; *Bh*, basihyal; *Ch*, ceratohyal; *Clei*, cleithrum; *Hy*, epilaterohyal (attached to the opercular); *Id*, infradentary; *Op*, opercular; *Op.i*, internal side of the opercular; *Pra*, prearticular; *Psp*, parasphenoid; *ioc*, infraorbital canal; *lc*, main lateral canal; *orb*, orbit; *p?oc*, pores presumably of the oral canal; *psoc*, pores of the supraorbital canal; *stc*, supraoccipital commissure.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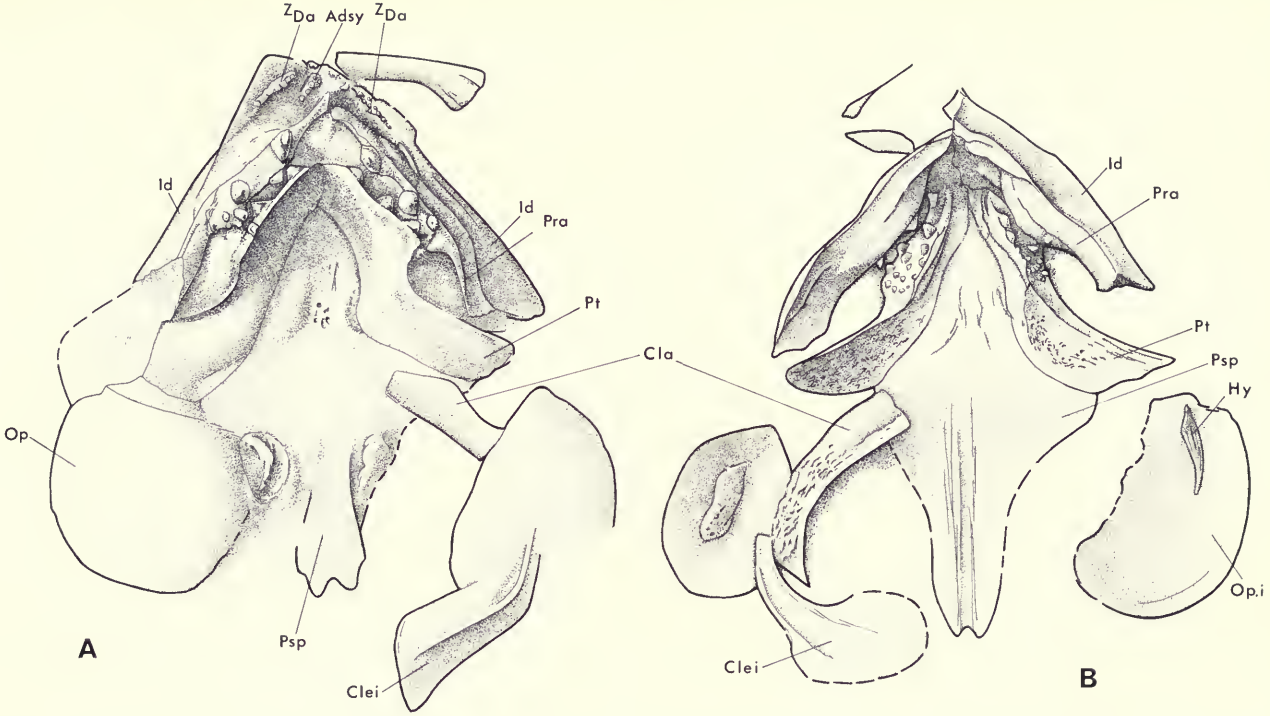

FIG. 5. *Megapleuron zangerli* n. sp., specimen Dab - (drawn from rubber casts); Middle Pennsylvanian/Pit 11, Will and Kankakee Counties, Illinois. Approximately ×6. **A**, dorsal view. **B**, ventral view. *Adsy*, adsymphysial plate; *Cla*, clavicle; *Clei*, cleithrum; *Hy*, epilaterohyal (attached to the opercular); *Id*, infradentary; *Op*, opercular; *Op.i*, internal side of the opercular; *Pra*, prearticular; *Psp*, parasphenoid; *Pt*, entopterygoid; Z_{Da}, tooth plate of the anterior dentary.

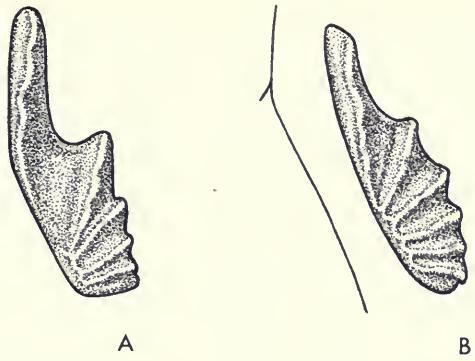

FIG. 6. Tentative restoration of the tooth plates in adult specimens of *Megapleuron zangerli* n. sp. A, lower jaw; B, upper jaw.

tween the posterior and the rostral portion of the skull roof has already been mentioned above.

The skull roof (figs. 4A, 7) can be restored fairly well. As in *M. rochei*, the most readily recognizable bone is E (R 5323, PF 3200) followed by a pair of C-bones between which the rostrad median tip of B extends. B surrounds the posterior part of the right C-bone in R 5323. Judging from PF 3200, the same is true for the left side so that B is much broader as restored in *M. rochei*. On the left side of the type specimen R 5323, bones are missing and the preserved ones seem to be pushed against the median line covering parts of B. J and I are small bones lateral to B; Z and Y are not larger. KX has one suture in common with C and may extend onto the posterolateral edge of E on the left side. Rostrad to KX on the left side, E is bordered by a long LM and a smaller N. In contrast, only one very long bone occupies the region between J and the middle of E on the right side; this bone may include K+L+M. Only bones 4 and 5+8 can be identified posterior to the orbit.

The sensory line system can be followed on the skull roof and on the body. The supraoccipital commissure (*stc*) passes through B and I near the posterior border of these bones. The bones around the main lateral line (*lc*) are not recognizable in the type specimen R 5323. Judging from specimen PF 3200 (fig. 7) the main lateral line passes through Z and Y (bones as long as their medial neighbors I and J) into KX where the infraorbital canal (*ioc*) and the supraorbital canal branch off. Large pores of the supraorbital canal (*psoc*)

open within LM of KLM respectively. Similarly, large pores can be seen in the rostrad part of the infradentary (fig. 4B; *Id*) which may be pores of the oral canal while the mandibular canal seems to cross the infradentary near the ventral border. The main lateral line could be found only on the middle of the flank (fig. 7). Neither dorsal nor ventral components of the lateral line system have been observed on the body.

The dentition is best preserved in specimen Dab - (fig. 5). The large rostral part of the parasphenoid (*Psp*) separates the entopterygoids (*Pt*) widely on the ventral and on the dorsal side so that the entopterygoids come into contact in a short symphysis only. A groove runs abrostrad on the ventral side of the parasphenoid so that the parasphenoid ends like a short swallowtail as known in some Devonian dipnoans. The postero-lateral wings of the entopterygoids are directed laterad and do not surround the lateral edges of the parasphenoid. The teeth are not yet fused as tooth plates in these juvenile specimens; four tooth rows can be counted on the entopterygoid in specimens PF 5707 and Dab -, six in specimen PF 3200. Rostrad to the entopterygoids, the vomer could be found in PF 3200 only (fig. 7). The existence of a pair of vomers could not be determined. The tooth rows of the prearticular (*Pra*) are opposed to the tooth rows of the entopterygoid (fig. 5). Very small teeth (fig. 5A) cover plates rostrad to the prearticulars; the paired tooth-bearing plates on the rostral border of the lower jaw are the anterior dentaries (Z_{Da}; for terminology see Schultze, 1969, pp. 52-55). These dentaries are also preserved in PF 8370. Small teeth indicate a tooth-bearing adsymphysial plate (*Adsy*) medial to the left anterior dentary. The outer surface of the lower jaw is formed—as far as can be judged from the specimens—by one large bone, the infradentary (*Id*), including anterior and posterior infradentaries and perhaps the posterior dentary.

It has been known since Semon (1901) that the tooth plates in dipnoans develop from isolated teeth arranged in rows. During ontogeny the teeth become larger, new teeth develop on the buccal end of the tooth row and new tooth rows are added abrostrally. This pattern can be seen in the specimens of *M. zangerli*, too. Four tooth rows with 3, 3, 2, 2 teeth in the rows from rostral to abrostral exist on the entopterygoid of the smallest specimen, PF 5707. On larger specimens, the number of teeth (Dab -: 4, 4, 4, 3) and the tooth rows (PF 3200: six tooth rows) are augmented. It is difficult to follow the development of the tooth plate on the prearticular because of its preservation. I count three rows on the prearticular of the speci-

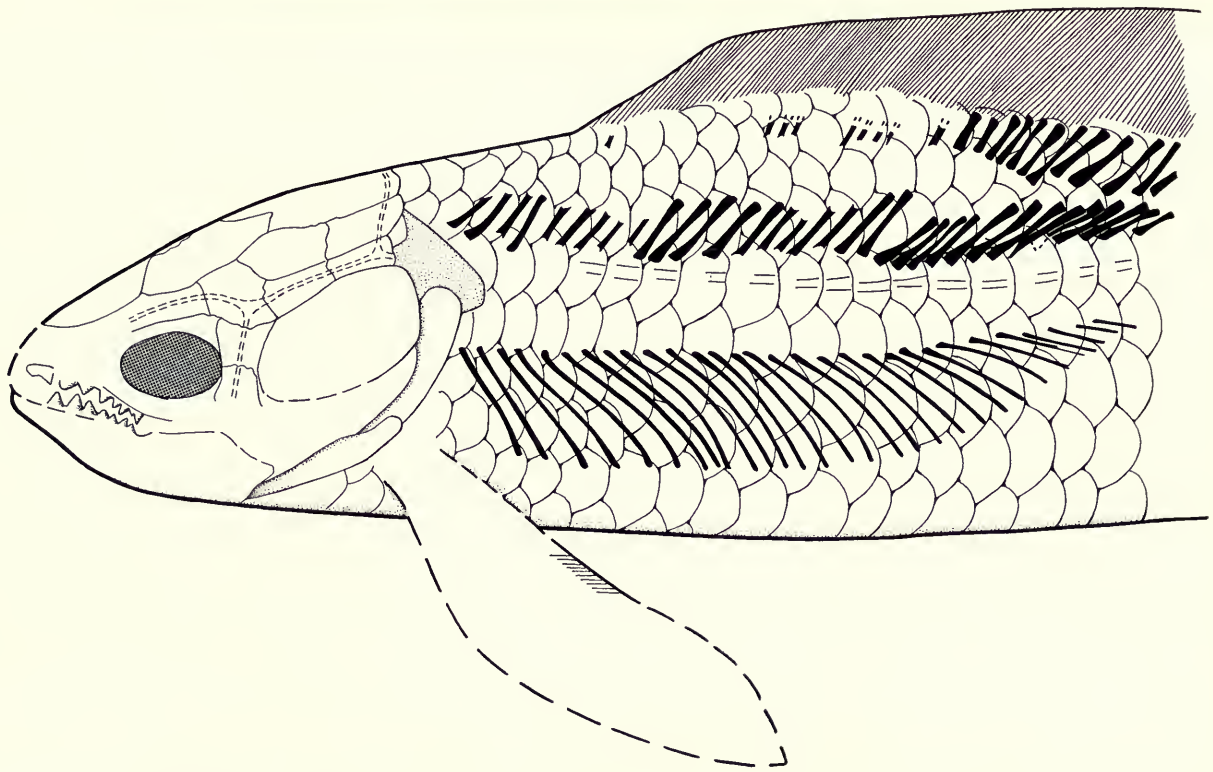

FIG. 7. *Megapleuron zangerli* n. sp., restoration of head and trunk in lateral view, based on specimen PF 3200; Middle Pennsylvanian/Pit 11, Will and Kankakee Counties, Illinois. Approximately × 4.

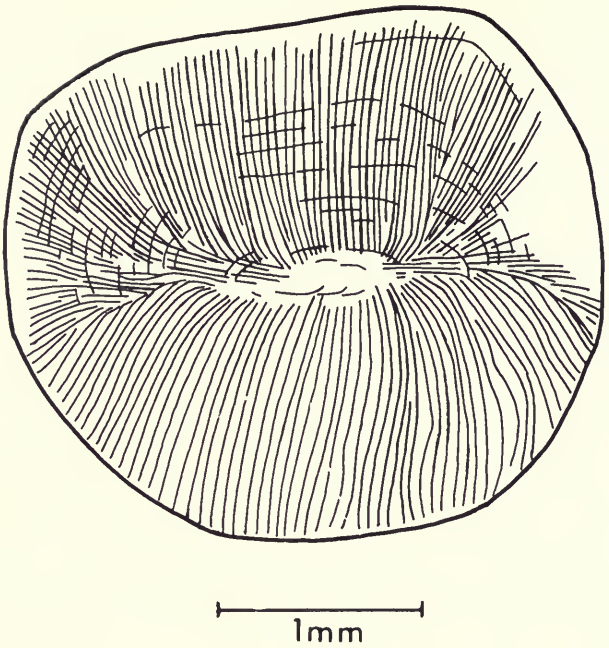

FIG. 8. *Megapleuron zangerli* n. sp., scale from the ventral region of the trunk, PF 3200; Middle Pennsylvanian/Pit 11, Will and Kankakee Counties, Illinois. × 12.5.

mens PF 5707, W 118, PF 8370, and Dab -. There are 2, 2, 1 (W 118) and 3, 2-3, 2 (Dab -) teeth in the rows; only the largest specimen PF 3200 shows more tooth rows (four to five), as on the entopterygoid. An attempt has been made based on the largest specimens, Dab - (fig. 5) and PF 3200, to restore the tooth plates of an adult *M. zangerli* (fig. 6). The restoration shows a gap between the first and the second tooth rows particularly evident in the tooth plate of the lower jaw (fig. 6A). This feature is unknown in *Sagenodus*-like tooth plates, which the tooth plates of *M. zangerli* most closely resemble. Such a gap is also not seen in small juvenile tooth plates of *Sagenodus* (Lund, 1970, fig. 8B, 8), showing that a rearrangement of tooth rows during ontogeny cannot be expected. Consequently, the restoration seems to be justified. The possibility of changing the anlage of the tooth rows is neither likely nor has it yet been observed.

Three elements of the hyoid arch are preserved in the type specimen (fig. 4B). An unpaired element, the basihyal (*Bh*), lies behind

FIG. 9. *Megapleuron zangerli* n. sp., juvenile specimens; Middle Pennsylvanian/ Pit 11, Will and Kankakee Counties, Illinois. × 3. A, PF 8369. B, W 118.

the symphysis followed by dislocated elongated bones with broadened ends, the ceratohyals (*Ch*). In the recent *Neoceratodus*, the cartilagenous part of the opercular is connected with the hyoid arch by the cartilagenous epilaterohyal ("the laterohyale of the epilaterohyale" Bertmar 1959="hyomandibulare" of Huxley). In *M. zangerli*, the laterohyal part (fig. 4B, 5B: *Hy*) of the epilaterohyal is ossified and fixed to the opercular, even in the smallest known specimen, PF 5707 (Denison 1969, fig. 110).

The opercular is elongated and is nearly twice as long as deep. Subopercular or gular plates could not be found.

The shoulder girdle consists of three elements: clavicle (*Cla*), cleithrum (*Clei*), and anocleithrum (*Aclei*). Clavicle and cleithrum

are elongated bones; the clavicle is enlarged ventromediad, the cleithrum dorsad where it overlaps the anocleithrum. The anocleithrum with the typical dorso-rostro-mediad-directed horn has been found in W 118, R 5323, and PF 3200.

The complete body is preserved in two specimens, PF 8369 (fig. 9A) and PF 8329; portions of the caudal region are missing to various degrees in all other specimens. Anal, caudal and dorsal fin form a continuous medial fin extending dorsally far rostrad. The dorsal fin also extends far rostrad in juvenile specimens of *Neoceratodus* (Semon, 1893, pl. 7, 8), but the development of the supporting endoskeleton below the rostral part of the dorsal fin in specimen PF 3200 and the formation of fin rays in the whole dorsal fin in PF 8370 and PF 3200 demonstrates that the rostrad extension of the dorsal fin is maintained in adult specimens of *M. zangerli.* The pectoral fin (fig. 9A, B) appears much earlier than the pelvic fin, as in *Neoceratodus* (Semon, 1893, pl. 7, 8 and p. 46). The pectoral fin has an elongated blade-like form. The endoskeleton in the paired fins could not be observed.

The notochord is unconstricted, and lacks ossifications around it, unless the stout elements posterior to the skull roof in specimen R 5323 (three shown in fig. 4A) represent neural arches. Neural spines, supraneurals, and about 30 ribs are developed; the endoskeleton ventral to the notochord in the caudal region is not preserved in any specimen.

The thin, round scales (fig. 8) are preserved best on the largest specimen PF 3200. The striation runs parallel to the length of the fish except at the dorsal and ventral edges, the transition area between the covered and the exposed portion of the scale. The distance between striae is greater on the exposed portion than on the covered portion of the scale. Growth lines could be observed on the covered portion.

The alimentary canal of specimen Dab - is filled with ostracods, a diet not uncommon in juvenile fishes and found in many small palaeoniscoids and acanthodians from Pit 11.

LATE PALEOZOIC DIPNOANS IN NORTH AMERICA AND EUROPE

The genus *Megapleuron* has not previously been reported in North America; other Carboniferous and Permian genera existing in both Europe and North America are *Sagenodus*, *Ctenodus*, and *Conchopoma* (Denison, 1969; Schultze, 1975). Complete speci-

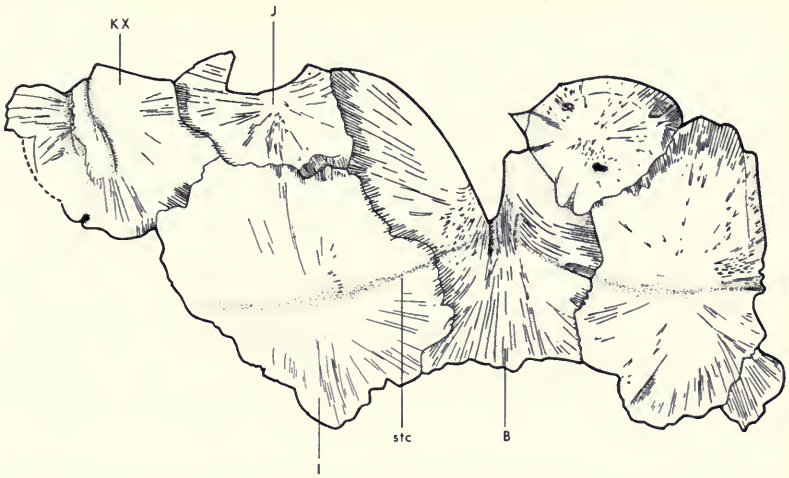

FIG. 10. *Sagenodus serratus* (Newberry), posterior portion of the skull roof AMNH 8645; Upper Coal Measures, Middle Pennsylvanian/Linton mine dump, Jefferson County, Ohio. × 2. B, I, J, KX, bones of the skull roof; *stc*, groove of the supraoccipital commissure.

mens of *Conchopoma* and *Megapleuron* are now known. In addition to isolated plates, tooth-plates and scales, the skull roof has been described in two species of *Sagenodus* from the Carboniferous of North America: *S. ohioensis* (Cope) (Cope, 1875, pl. 45, fig. 2) and *S. serratus* (Newberry) (Romer and Smith, 1934, fig. 4A, B). The skull roof AMNH 8645 (fig. 10) assigned by Cope (1875, pl. 42, fig. 5) to *Peplorhina anthracina* belongs to *S. serratus* (Denison, 1969, p. 195). The outline of B on the outer surface caused by extensive overlapping of I and J is the same as that described for *S. serratus* by Romer and Smith (1934, p. 709). The groove for the supraoccipital commissure (*stc*) is not as deep as that in the specimen described by Romer and Smith (1934). The main differences between *S. serratus* and *ohioensis* are in size and the postulated absence in *S. ohioensis* of the I-bone seen in *S. serratus*. The occipital region is missing in all three specimens assigned to *S. ohioensis*. If the figures of *S. ohioensis* (Cope, 1875, pl. 45, fig. 2; and Newberry, 1889, fig. 3) are compared with the figure of *S. serratus* (Romer and Smith, 1934, fig. 4A, B), one can observe that only the broad rostral part of B is preserved in *S. ohioensis*, and that a portion of the I-bone is present posterior to the right J-bone. This means that the normal *Sagenodus* pattern applies in *S. ohioensis*, too. In consequence, *S. ohioensis* and *S. serratus* could be conspecific.

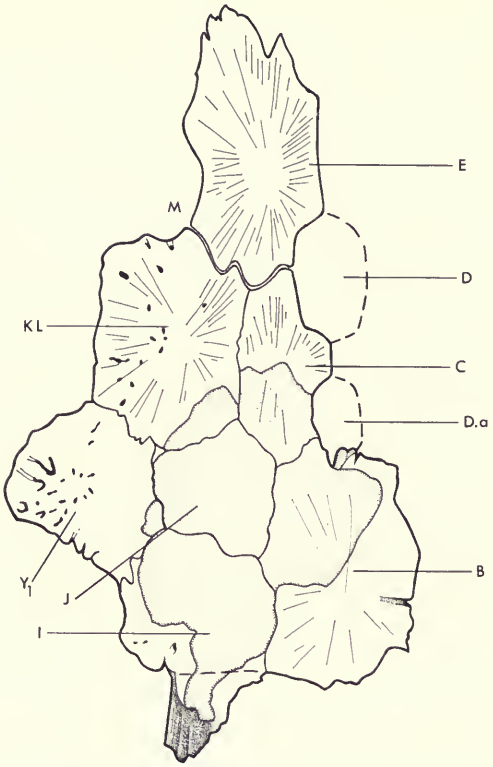

FIG. 11. *Ctenodus cristatus* Agassiz, skull roof PU 20466; Pomquet formation, Mabou group, Lower Pennsylvanian/shore south of Grand Etang, Inverness County, Nova Scotia, Canada. × 1. B, C, D, E, I, J, KL, M, Y_1, bones of the skull roof; *D.a*, additional D-bone.

A skull roof of *Ctenodus* has not yet been described from North America. Two specimens are known to me: a plaster cast (AMNH 8593) of a specimen from the Carboniferous of Ohio and the specimen PU 20466 from the Lower Pennsylvanian of Nova Scotia. The left half of the skull roof is preserved in PU 20466 (fig. 11). The left bone of the pair of C-bones and likewise the left bone of the pair of E-bones lie in front of the rectangular B. Two D-bones are developed, an individual variation. As in *C. cristatus* (Watson and Gill, 1923, fig. 21), J is smaller than I, and Y_1 and KL are large bones. Except for the occurrence of two D-bones, there is only a minor difference in the outline of B between PU 20466 and *C. cristatus*, a difference that lies within the variability of the species. It seems reasonable to assign this specimen to *Ctenodus cristatus* Agassiz.

Regarding temporal and geographic distribution of dipnoans, four genera are found in the late Paleozoic of North America but not in Europe, in addition to genera occurring on both continents (see above). The phylogenetic line leading to the recent Lepidosirenida seems to be represented by two genera, *Gnathorhiza* and *Monongahela* (Carlson, 1968; Lund, 1970) in North America only. *Tranodis* from the Mississippian of North America seems to be closely related to *Ctenodus*, and *Straitonia* from the Lower Carboniferous of Europe to *Sagenodus* (Thomson, 1965). Though the data are too scarce to establish or deny relationships, one can say that many features developed parallel and separately in post-Devonian time. *Uronemus* is restricted to Europe. *Conchopoma* and *Megapleuron* represent single genera of separate phylogenetic lines going back into the Devonian. For *Megapleuron* the closest comparison could be found in Devonian forms like *Phaneropleuron* or *Scaumenacia.*

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ADDENDUM

The so-called "blade" is a very common element in the Essex fauna from Pit 11. Bardack (1974) assigned this larval form to the dipnoans as *Esconichthys apopyris.* He cites (1974, pp. 989, 992) many characters which set *Esconichthys* apart from known dipnoans, and uses vague features (p. 992: "body outline, gill form, size of the eye, form of the mouth, etc.") to justify the position of *Esconichthys* within the dipnoans. A reduced number of gills as in *Esconichthys* can be found only in amphibians, and the elongation of one pair together with scant development of pinnulae is known only in those recent amphibians with a long development in the egg, uterus or brood sac (Wunderer, 1910; Rauther, 1937). It is not possible to use ontogenetical features of dipnoans to distinguish *Esconichthys* from amphibians, because even very recent investigations of the ontogeny of *Neoceratodus* (Fox, 1965) demonstrate so many similarities between dipnoans and amphibians that it is understandable that, in earlier time, the dipnoans were considered as ancestral to the amphibians. However, if larvae of amphibians have to be excluded because no adult individuals are known from contemporary non-marine deposits (Bardack, 1974, p. 992), dipnoans have to be excluded even more stringently because larvae and adults very different from *Esconichthys* are indeed known from contemporary deposits. The known dipnoan larvae of *Megapleuron* (see above) and *Conchopoma* (Denison, 1969) from the Essex fauna also show all features characterizing larvae of recent dipnoans. I have no idea about the systematic position of *Esconichthys* within the chordates. Concerning the two paired hard structures in the head region, I agree with Bardack (1974, p. 992): "No similarly shaped cranial structure is known to the author" within the chordates.

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